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CLIMATE RESILIENCE IN PEARL MILLET AND GENOMIC RESOURCES

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ABSTRACT:

Pearl millet [Pennisetum glaucum (L.) R. Br.] is the sixth most important cereal crop after rice, wheat, maize, barley and sorghum. It is widely grown on 30 million ha in the arid and semi-arid tropical regions of Asia and Africa, accounting for almost half of the global millet production. Climate change affects crop production by directly influencing biophysical factors such as plant and animal growth along with the various areas associated with food processing and distribution. Assessment of the effects of global climate changes on agriculture can be helpful to anticipate and adapt farming to maximize the agricultural production more effectively. Pearl millet being a climate-resilient crop is important to minimize the adverse effects of climate change and has the potential to increase income and food security of farming communities in arid regions. Pearl millet has a deep root system and can survive in a wide range of ecological conditions under water scarcity. It has high Photosynthetic efficiency with an excellent productivity and growth in low nutrient soil conditions and is less reliant on chemical fertilizers. These attributes have made it a crop of choice for cultivation in arid and semi-arid regions of the world; however, fewer efforts have been made to study the climate-resilient features of pearl millet in comparison to the other major cereals. Several hybrids and varieties of pearl millet were developed during the past 50 years in India by both the public and private sectors. Pearl millet is also nutritionally superior and rich in micronutrients such as iron and zinc and can mitigate malnutrition and hidden hunger. Inclusion of minimum standards for micronutrients—grain iron and zinc content in the cultivar release policy—is the first of its kind step taken in pearl millet anywhere in the world, which can lead toward enhanced food and nutritional security. The availability of high-quality whole-genome sequencing and re-sequencing information of several lines may aid genomic dissection of stress tolerance and provide a good opportunity to further exploit the nutritional and climate-resilient attributes of pearl millet. Hence, more efforts should be put into its genetic enhancement and improvement in inheritance to exploit it in a better way. Thus, pearl millet is the next-generation crop holding the potential of nutritional richness and the climate resilience and efforts must be targeted to develop nutritionally dense hybrids/varieties tolerant to drought using different omics approaches.

INTRODUCTION:

The changing climate is leading to an increase in global average temperature affecting agricultural production worldwide. Further, it directly influences biophysical factors such as plant and animal growth along with the different areas associated with food processing and distribution. Assessment of effects of global climate changes and deployment of new tools and strategies to mitigate their effect is crucial to maximizing agricultural production to meet out food demands of the increasing population. In this context, pearl millet is most useful as it is a nutritious, climate change-ready crop with enormous potential for yielding higher economic returns in marginal conditions in comparison with other cereals even in case of climate change with harsh temperature conditions. Moreover, it has greater ceiling temperatures for grain yield and is an underutilized crop with huge nutritional potential, which needs to be utilized fully (Krishnan and Meera, 2018). It is more resilient to extreme climatic events such as drought and water scarcity and can play a vital role in ensuring food and nutritional security in changing climatic scenarios, which is mounting to frightening proportions.

Globally, it is the sixth most significant cereal crop after rice (Oryza sativa), wheat (Triticum aestivum), maize (Zea mays), barley (Hordeum vulgare) and sorghum (Sorghum bicolor). It is a staple food of 90 million poor people and extensively grown on 30-million-ha area in the arid and semi-arid tropical regions of Asia and Africa. It is also used for feed and fodder and accounts for almost half of the global millet production (Srivastava et al., 2020a). It is mainly cultivated on marginal lands under rainfed conditions and can sustain and produce a significant amount of grain even in drought-prone areas that receive an average annual precipitation of <250 mm (Nambiar et al., 2011). It surpasses all other cereals such as wheat, maize, rice, sorghum and barley because of its unique attributes like the C4 plant having high photosynthetic efficiency, more dry matter production capability, and survival under adverse agro-climatic conditions with lesser inputs and more economic returns (Nambiar et al., 2011). C4 plants have more ability to fix inorganic CO_2 and more efficient in water utilization in comparison with C3 plants due to the presence of "Kranz" anatomy in leaves. Thus, being a C4 plant, pearl millet can account for

30% of global terrestrial carbon fixation along with other C4 plants such as maize and sorghum (Choudhary et al., 2020). It also possesses several advantages such as early maturity, drought tolerance, the requirement of minimal inputs, and usually free from biotic and abiotic stresses. Its inherent ability to endure high temperatures up to 42°C during the reproductive phase makes it suitable for growth in extremely hot summers under irrigations in northern Gujarat and eastern Uttar Pradesh of India, thus making it a climate-resilient crop. It also possesses the huge capability to eliminate micronutrient deficiency among developing countries (Rai et al., 2012; Anuradha et al., 2017; Singhal et al., 2018) as it supplies 30–40% of inorganic nutrients and bestows affordable staple food along with ample amounts of iron and zinc (Rao et al., 2006). It has very high nutritional values and is a good source of energy, carbohydrates, crude fibers [resistant starch (RS), soluble and insoluble dietary fibers], soluble and insoluble fat, proteins (8–19%), ash, dietary fibers (1.2 g/100 g), antioxidants and fat (3–8%) with better fat digestibility, iron, and zinc in comparison with other major cereals (Uppal et al., 2015). It is also a rich source of vitamins such as riboflavin, niacin, and thiamine and minerals (2.3 mg/100 g) such as potassium, phosphorous, magnesium, iron, zinc, copper, and manganese (Weckwerth et al., 2020). It exhibits a better essential amino acid profile of protein in comparison with other cereals such as maize and rice. It contains lesser cross-linked prolamins leading to higher digestibility of the millet proteins. It has 74% polyunsaturated fatty acids (PUFAs) and rich in nutritionally sought-after omega-3 fatty acids such as oleic acid (25%), linoleic acid (45%), and linolenic acid (4%), which are considered best for health (Rooney, 1978; Nantanga, 2006; Dyall, 2015; Singh et al., 2018). It is a gluten-free grain that retains alkaline properties even after being cooked and is thus good for people suffering from gluten allergy. It owns a higher quantity of slowly digestible starch (SDS) and RS that account for lower glycemic index (GI) and is much preferred in recent times of transforming diets, food habits and the food industry (Satyavathi et al., 2020). It is a highly nutritious, non-acid-forming, non-glutinous food having several nutraceuticals and health beneficial properties along with high fiber content. It acts as a probiotic food for microflora present in our body and keeps us away from constipation. It is also capable of lowering cholesterol due to the presence of niacin in its grain. It contributes to an antioxidant activity with phytates, polyphenols etc. Consumption of various types of millets is considered to protect against certain types of cancer, cardiovascular diseases and various age-related diseases. Due to these useful properties, pearl millet is gaining a lot of popularity among health-conscious people all over the world. Due to its nutritional properties, pearl millet has been renamed as nutri-cereal (Gazette of India, No. 133 dated 13 April, 2018) and can play a vital role in overcoming malnutrition and ensure food and nutritional security.

RESULTS:

Status of Pearl Millet Production:

Pearl millet is a descendent of the wild West African grass and was domesticated over 4,000 years ago in the West African Sahel, spreading later to East Africa and India (Sharma et al., 2021). Now it is being cultivated over 30 million ha worldwide, with the majority of the crop grown in Africa (>18 million ha) and Asia (>10 million ha) (Raheem et al., 2021). It is extensively cultivated in India and is the fourth most extensively grown cereal crop after rice, wheat and maize. Rajasthan, Maharashtra, Uttar Pradesh, Gujarat, and Haryana are the major pearl millet-growing states, contributing 90% of the total production in India. Out of this, Rajasthan contributes a maximum of around 4.283 million 5 tonnes, followed by Uttar Pradesh (1.302), Haryana (1.079), Gujarat (0.961), Maharashtra (0.66), and Tamil Nadu (0.084). It is mainly cultivated in the rainy (kharif) season (June/July-September/October) but it is also grown in some parts of Gujarat, Rajasthan, and Uttar Pradesh during the summer season (February-May), while it is also cultivated in states of Maharashtra and Gujarat at a small scale during the post-rainy (rabi) season (November-February). As millets are climate-smart crops with nutritional value, they are rightly termed as nutricereals (Gazette of India, No. 133 dated 13 April, 2018). In addition, to include millets into the mainstream and exploit its nutritionally superior qualities and promote its cultivation, Government of India has declared Year 2018 as the "Year of Millets" and FAO Committee on Agriculture (COAG) forum has declared Year 2023 as "International Year of Millets."

Pearl Millet Improvement:

Indian Council of Agricultural Research started pearl millet breeding in India in the 1940s, and X1 and X2 were the two chance hybrids released in India for commercial utilization in the fifties (Yadav and Rai, 2013). Pearl millet improvement programs were implemented in several phases. During phase I, breeders mainly focused on the flowering habit, mode of pollination, germplasm evaluation and enhancement, genetics and cytogenetics of agronomically important traits, cytoplasmic male sterility (CMS) etc. Thus, initially, efforts were put forward towards the identification and use of dwarfing genes for enhancing the yield using locally adapted materials and various Open Pollinated Varieties (OPVs) were developed. As a result of this, pearl millet hybrid research has gained importance in India and the productivity was 4.5 kg/ha/year during this phase (Yadav et al., 2019). By the 1960s, hybrid development became the major objective of breeding for enhancing pearl millet production and productivity. Hybrid "HB-1" (Hybrid Bajra-1) was the first pearl millet hybrid released in 1965 (Athwal, 1965) followed by a series of hybrids between 1965 and 1988 and during phase II, an annual increase of 6.6 kg/ha was achieved in productivity. These improvement is due to the combined contribution of the development of high-yielding hybrids, varieties, biofortified genotypes, improved production practices, technologies, and recommendations coupled with adoption by farmers. Pearl millet is the first crop in which marker-assisted-selection (MAS) strategies and tools were applied to get improved varieties. Yadav et al. (2021) discussed various past strategies and future approaches to accelerate genetic gains to meet future demand. Further, they also emphasized the importance of genome editing, pre-breeding, precision phenotyping protocols and speed breeding approaches for pearl millet improvement and enhanced genetic gains. On the other hand, due to a lack of knowledge and non-availability of ideal dose of fertilizer among poor farmers, it becomes difficult to harvest the real yield potential. Hence, the yield improvement of pearl millet under low nitrogen input is indeed beneficial for economic and environmentally sustainable cultivation. Pujarula et al. (2021) studied the genetic variation for nitrogen-use efficiency (NUE) among a set of 380 diverse pearl millet lines. Thus, such studies of different physiological traits and their relationship with grain yield are very important for understanding the complex nature of NUE.

DISCUSSION:

Pearl millet can survive and produce a large quantity of grain, whereas other cereals such as rice, wheat, maize, sorghum and barley may fail to provide economic benefits under adverse conditions and poor soil. It can provide multiple securities in form of food, fodder, livelihood, nutrition health and ecological benefits, whereas wheat and rice provide only food security, thus making it a crop of agricultural security. Its ability to withstand higher temperature and survival in drought-prone areas and cultivation in parts of Gujarat and eastern Uttar Pradesh of India during hot summers makes it a climate-resilient crop for overcoming the adverse effects of the changing climate (Gupta et al., 2015). National Agricultural Research System (NARS) in India and International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) have played a significant role in developing various improved breeding and parental lines of prospective hybrids. A total of 21,392 germplasm accessions, including 750 accessions of wild species of genera Pennisetum and Cenchrus,
collected from 50 countries are conserved at the ICRISAT Genbank, while 8,284 accessions are conserved at the National Bureau of Plant Genetic Resources (NBPGR), New Delhi, India. These lines have been widely used in breeding programs in both the public and private sectors for the development and commercialization of a large number of hybrids (public 70 and private sectors 105 were under cultivation in 2019). Debieu et al. (2018) also performed GWAS on a panel of 188 inbred lines of West Africa to identify QTLs associated with stay-green trait and biomass production in early drought stress conditions. In addition, different "omics" technologies such as transcriptomics, proteomics, metabolomics can be also useful for quantitative and qualitative analyses of gene expression allowing more precise use of MAS and transgenic technologies. RNA sequencing (RNA-Seq) is widely used among the different transcriptome analysis methods as it can efficiently detect unknown genes and novel transcripts and has much potential to study gene expression and their regulating pathways (Hrdlickova et al., 2017). The transcriptome analysis of pearl millet can reflect new prospects into gene regulatory networks existing in this crop under abiotic stress conditions. Stress-regulated pathways in pearl millet can be studied by the detection and characterization of stress-responsive genes via transcriptomics

and then different approaches can be followed for improving stress tolerance/resistance in millet (Mishra et al., 2007). Several transcriptomic studies in pearl millet have been used to reveal the functions of some salinity stress-responsive genes such as PgDHN, PgDREB2A, PgVDAC, PgNHX1 (Desai et al., 2006; Mishra et al., 2007; Verma et al., 2007; Agarwal et al., 2010; Reddy et al., 2012; Singh et al., 2015). Recently, complete transcriptome analysis has been done in pearl millet for drought stress response (Dudhate et al., 2018; Jaiswal et al., 2018; Shivhare et al., 2020). Dudhate et al. (2018) unraveled the molecular mechanism governing drought tolerance in two pearl millet inbred lines, ICMB 843 and ICMB 863, using RNA-Seq approach, and it is the first report of the study of drought tolerance by RNA sequencing in pearl millet. More recently, an important study on RNAseq analysis was performed to assess the comparative transcriptomics at the vegetative and flowering stage in a drought-tolerant (PRLT2/89-33) genotype to discover underlying genes to drought tolerance (Shivhare et al., 2020).

Proteomics is another important technology to get information on protein concentrations, post-translational modifications (PTMs), protein–protein interaction, structures linked with stress tolerance, regulatory functions of proteins encoded by genes (Ghatak et al., 2017). Identification and characterization of stress-responsive genes and their proteins from pearl millet can help in defining stress-regulated pathways. Further, it can help design strategies to improve stress tolerance/resistance of pearl millet as well as other related crop plants. Several proteomic studies have been also carried out in pearl millet, which can provide a framework to investigate C4 photosynthesis in pearl millet in more depth (Ghatak et al., 2016, 2021; Weckwerth et al., 2020). A shotgun proteomics approach (GEL-LC-Orbitrap-MS) was used by Ghatak et al. (2016) to identify 2,281 proteins from different tissues of pearl millet (root, seed, and leaf) showing significant changes under drought stress condition. Thus, a lot of information has been generated for the improvement of this crop but still, there is a big challenge to identify various crucial genes responsible for its adaption to survival under different abiotic stresses conditions. In addition, the identification of genomic regions governing NUE and its use in pearl millet breeding programs via MAS can be also exploited for survival under adverse conditions. Moreover, exploring several new and advanced genomic tools will be also beneficial for the advancement of this crop to harness its suitability to adverse conditions and utilize its inbuilt capacity to ensure global food and nutritional security.

Table No. 1: Achievement and Milestones in pearl millet improvement through conventional/heterosis breeding

Year	Achievements	References
1940	Indian Council of Agricultural Research started Pearl millet breeding in India.	Yadav and Rai, 2013; Singh et al., 2014
1950	X1 and X2 were the two chance hybrids released in India for commercial utilization.	Yadav and Rai, 2013; Singh et al., 2014
1965	First pearl millet hybrid, Hybrid "HB-1" (Hybrid Bajra-1) was released.	Athwal, 1965
1965	Establishment of the ICAR-All India Coordinated Research Project on Pearl Millet	Yadav and Rai, 2013
1997-2008	Effective phenotypic screening techniques and resources were developed, and resistance breeding programs were developed.	Thakur and King, 1988; Singh et al., 1997; Hash et al., 1999; Hash and Witcombe, 2002; Jones et al., 2002; Thakur et al., 2008
1974-2020	Identification and release of 175 hybrids and 62 varieties for cultivation in different agro-ecological zones of India	Satyavathi et al., 2020
2018	Identified heterotic groups for grain yield and a total of 343 hybrid parental [maintainer (B-) and restorer (R-)] lines were genotyped with 88 polymorphic SSR markers.	Ramya et al., 2018
2021	Genetic variation studies for NUE among a set of 380 diverse pearl millet lines	Pujarula et al., 2021
2021	Studied expression of heat stress-responsive gene Pghsp	Sankar et al., 2021

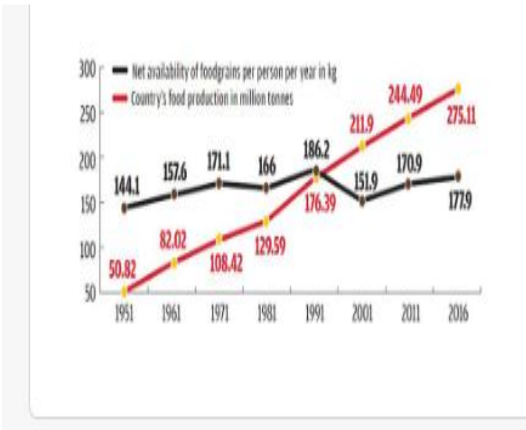
Table No. 2: Achievements and milestones in pearl milet improvement molecular and advanced genomic tools

Year	Achievements	References
Molecular markers		
1994	Study of 200 samples of varied pearl millet lines using RFLP markers to reveal polymorphism	Liu et al., 1994
1995	Development of amplified fragment length polymorphism (AFLP) markers for pearl millet using nuclear genomic sequences	Devos et al., 1995
2000	163 AFLP markers were used to study genetic variability within and between pearl millet landraces	Busso et al., 2000
2001	Development of STSs markers from BAC clones	Allouis et al., 2001; Qi et al., 2001
2002	Genetic diversity was studied within and between 504 landraces of core collection using RFLP probes	Bhattacharjee et al., 2002
2003	18 SSR markers were developed from genomic sequences in pearl millet	Budak et al., 2003
2004	A consensus map of 353 RFLP and 65 SSR markers was developed for the first time.	Qi et al., 2004
2005	SSCP-SNP primes were developed from pearl millet EST collections	Bertin et al., 2005
2008	EST-based SSRs were developed in pearl millet	Senthilvel et al., 2008
2011	DArT platform was established for pearl millet, and 574 polymorphic DArT markers were mapped and used to genotype a set of 24 diverse pearl millet inbred lines	Supriya et al., 2011
2012	Conserved intron-specific primers (CISP) were developed from EST sequences using parents of two mapping populations for 18 genes	Sehgal et al., 2012

Nutritional Security:

Food grain production has increased but still, to feed the growing population and meeting out good health of the people in the present situation, nutritional security is very important (Figure 3).

Figure 3: Trends in food grain production and per capita availability in India. Adapted from: Agriculture Statistic, Ministry of Agriculture and Family Welfare.



It is also called the “Powerhouse of Nutrition” due to its richness with essential nutrients in good quantity and quality, which are vital for leading healthy and nutritious life. Pearl millet has elevated contents of various macronutrients as well as micronutrients like iron, zinc, magnesium, calcium, phosphorous, copper, manganese, riboflavin, and folic acid. Owing to such excellent nutritional values, it is gaining popularity and is preferred by people all over the world including developed countries. Despite its nutritional superiority, the consumption of pearl millet flour is restricted to very few specific regions of the world because of the poor shelf life of the flour and the development of rancidity or off-odor on storage (Rani et al., 2018). Rancidity is caused by oxidative/hydrolytic enzymes such as lipase, lipoxygenase (LOX), etc., where they hydrolyze the triacylglycerol (TAG) to diacylglycerols, glycerol, monoglycerol, and free fatty acids (Manley and Mayer, 2012). It is also enriched with many essential amino acids except lysine and threonine and has relatively higher methionine. Being gluten-free, it is extremely useful for people suffering from celiac diseases who are generally allergic to the gluten content of wheat and other cereals. Pearl millet is exceptionally useful for people suffering from diseases like diabetes, obesity, diabetic heart disease, atherosclerosis and metabolic diseases due to its health beneficial properties (Kumar et al., 2020). The success of pearl millet biofortification program lies in the high-throughput precision phenotyping for the estimation of grain micronutrient content. Further, demonstration of the feasibility of developing high-Fe and high-yielding hybrids and encouraging the partners to breed for these micronutrient traits by means of mainstreaming the biofortification can be an important approach for its promotion. There is a high need to facilitate the focused screening of partners breeding materials for grain Fe and Zn contents for their introgression of high Fe content into locally adapted, high-yielding and farmer-preferred cultivars. Promotion and strengthening of the pipeline of high-iron and high-yielding partners-bred hybrids and testing of their grain samples for grain Fe and Zn contents can be a useful step for enhancing its importance. In addition to this, bioavailability is another aspect that needs to be focused to get full potential of this crop.

Table No.3: Nutritional comparison of pearl millet with sorghum, rice and wheat (in 100 g grain)

Contents	Crop			
	Pearl millet	Sorghum	Rice	Wheat
Carbohydrates (g)	61.8	67.7	78.2	64.7
Protein (g)	10.9	09.9	07.9	10.6
Fat (g)	5.43	1.73	0.52	1.47
Energy (Kcal)	347	334	356	321
Dietary fiber (g)	11.5	10.2	02.8	11.2
Calcium (mg)	27.4	27.6	07.5	39.4
Phosphorus (mg)	289	274	96	315
Magnesium (mg)	124	133	19	125
Zinc (mg)	2.7	1.9	1.2	2.8
Fe (mg)	6.4	3.9	0.6	3.9
Thiamine (mg)	0.25	0.35	0.05	0.46
Riboflavin (mg)	0.20	0.14	0.05	0.15
Niacin (mg)	0.9	2.1	1.7	2.7
Folic acid (µg)	36.1	39.4	9.32	30.1

Adapted from: NIN, Hyderabad, 2018.

Challenges for Pearl Millet:

Despite the breeding efforts, most of breeding programs fail to deliver hybrids due to a vast variation in microclimate (day and night temperature and humidity) and soil apart from rainfall, which requires proper quantification. Further, narrow cultivar diversity in drought-prone ecology also is another factor for this. Thus, there is a high need to give higher priority to the below-mentioned areas to promote its production and utilization:

- Development of hybrids/varieties of pearl millet with better regenerative capacity on reversal of dry spell for harsh environment/drought-prone areas (for A1 zone in India).
- Development of hybrids/varieties resistant/tolerant to salt/high temperature.
- Shift in focus of breeding from productivity improvement to the identification of end product-specific traits.
- Mainstreaming of biofortification in pearl millet for iron and zinc.
- Enhancement of shelf life of pearl millet flour and overcome rancidity to promote its products.
- Development of screening protocols and control measures against different diseases such as downy mildew, blast, rust, ergot, smut.
- Generating authentic data on nutritional benefits of pearl millet and bioavailability studies.
- A study on demand survey for pearl millet.

CONCLUSION:

Pearl millet being a climate-resilient crop along with high nutritional value can be exploited for improving nutritional quality and combating malnutrition. It is almost free from major diseases and insect attacks and could be cultivated with a good harvest. Hence, the focus should be laid towards the development of food products from pearl millet to make it acceptable as an alternative crop of the future. Indian policymakers need to refocus their interest toward millet farming systems and policies should be engraved for creating a feasible environment for pearl millet farmers. After the successful use of genomic tools, screening and development of improved genotypes have become easy and fast, and the progress toward enhancing the use of genomic resources is quite appreciable. But it can be characterized further for harnessing the natural genetic variation within the germplasm, and a lot of efforts are still required to execute genomics to improve the crop using high-throughput genome analysis, sequence-based molecular markers, NGS techniques and genome editing etc. The genomics and breeding platform needs a better alignment and constant up-gradation to develop improved hybrid parental lines, and populations must be adapted specifically according to the specific global agro-ecologies. The idea of genetic gains, genome editing, pre-breeding, and speed breeding can be also very useful for the researchers in selecting plants for desired traits along with many variations. On the other hand, the construction of high-density maps, QTL detection, candidate gene identification, new genome sequence techniques, use of advanced multi-parental and AM panels, GWAS and GS can speed up the recognition of allelic variants for pearl millet improvement. Mapping of several abiotic stresses, QTLs, etc. is highly desired to combat global climatic effects and the recently developed technologies must be tested under actual conditions.

The outcomes from model crops can be used in pearl millet to achieve added improvement and develop Zn- and Fe–enriched biofortified varieties. Synteny studies can prove useful for the identification of common genes linked with nutrition biosynthesis pathways, and these should be incorporated into pearl millet by traditional breeding or transgene techniques for further nutritional improvements. In addition, nutritional as well as the economic security of small and marginal farmers, enhancing demand of pearl millet, value addition and market-led extension through food science and nutrition is vital to promote the cultivation and consumption of this crop. In conclusion, multidisciplinary approaches, including breeding, genomics, bioinformatics, biotechnology, nutrition and genetics etc. are required to exploit and harness the beneficial attributes of nutricereal pearl millet for combating changing climate and attaining nutritional security.

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